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# Review. Biology and Systematics of the form genus *Rhizoctonia*

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## Abstract

Members of the form genus *Rhizoctonia* D.C. are considered as a complex mixture of filamentous fungi, having in common the possession of a non-spored imperfect state, usually referred to as the *Rhizoctonia* anamorph. The group includes several of the most devastating crop pathogens like *Thanatephorus cucumeris* (Frank) Donk (anamorph = *Rhizoctonia solani* Kühn), the majority of orchid mycorrhizal symbionts (mainly belonging to genus *Ceratobasidium* D.P. Rogers) and a collection of saprotrophic organisms of different systematic placement. The *Rhizoctonia* anamorph is characterized by several common features present among members of the entire *Rhizoctonia* species complex. Taxa from the group have been rearranged into several groups of higher fungi, including both Ascomycota and Basidiomycota, and split into several genera, employing criteria such as the analysis and ultrastructural comparison of septal apparatus. Until very recently, classification for some of the groups within the complex has been exclusively based on criteria such as hyphal anastomosis, since other types of diagnostic features are usually scarce in these fungi. Phytopathological studies in the complex have represented the major contingent of contributions in the group, especially in the case of *R. solani.* Some members of the complex have been reported to be protective isolates against pathogenic members of *Rhizoctonia* and some other fungal pathogens. This review focuses on the knowledge of several aspects of the species of *Rhizcotonia s. lato,* such as its current taxonomic placement, the biology and systematics of some groups of the complex, and a revision of the methodologies employed in studying it.

**Additional key words:** Basidiomycetes, biocontrol*, Ceratobasidiaceae, Ceratobasidium,* fungal diseases, methodology, taxonomy, *Thanatephorus.*

## Resumen

### Biología y Sistemática del género forma *Rhizoctonia*

Los miembros del género forma *Rhizoctonia* D.C. son considerados como un complejo de hongos filamentosos, presentando en común una fase asexual no productora de esporas, denominada anamorfo tipo *Rhizoctonia.* El grupo incluye algunos importantes patógenos como *Thanatephorus cucumeris* (Frank) Donk (anamorfo=*Rhizoctonia solani* Kühn), la mayoría de especies micorrícicas de orquídeas (principalmente del género *Ceratobasidium* D.P. Rogers), y algunos taxones de posición taxonómica variada. El anamorfo tipo *Rhizoctonia* es definido por una serie de características, presentes y comunes en todos los taxones del complejo. Los taxones del grupo han sido distribuidos entre varios grupos de hongos, incluyendo Ascomicetes y Basidiomicetes, y reubicados en varios géneros de ambas clases, empleando criterios de clasificación tales como el análisis y comparación de la ultraestructura del aparato septal. Habitualmente, la clasificación en algunos de los grupos del complejo ha estado basada en la aplicación de criterios tales como la anastomosis hifal, debido a que en este tipo de hongos es escasa la presencia de un número aceptable de caracteres diagnósticos. Los trabajos fitopatológicos en el complejo representan el mayor contingente dentro de las contribuciones publicadas, especialmente en el caso de *R. solani.* Algunos de los miembros del complejo son citados como protectores contra miembros patógenos de *Rhizoctonia* y otros patógenos fúngicos. El presente trabajo presenta los conocimientos actuales sobre aspectos del complejo, tales como su clasificación actual, la biología y sistemática de algunos de los grupos de *Rhizoctonia s. lato,* además de una revisión de las metodologías más comúnmente empleadas en su estudio.

**Palabras clave adicionales:** Basidiomycetes, biocontrol*, Ceratobasidiaceae, Ceratobasidium,* enfermedades fúngicas, metodología, taxonomía, *Thanatephorus*.

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## Introduction

The form genus *Rhizoctonia* is considered as an heterogeneous assemblage of filamentous fungal taxa that do not produce asexual spores and share a number of common features in their anamorphic states. The organisms belonging to this species complex are generally soil fungi, mostly associated with roots and usually pathogens, although there have been reports of a number of saprophytic and symbiotic taxa. Fungi in the form genus are distributed worldwide in both agricultural and forest soils and include some of the most economically important plant pathogens, causing foliar and root rot diseases of major crops.

The genus concept in *Rhizoctonia* was first established by De Candolle (1815). This concept was reviewed by Parmeter and Whitney (1970) more than a century later, who concluded that, according to De Candolle, the basic characters of the genus named by the Swiss author could be summarized in the production of sclerotia of uniform texture and association of the mycelium with roots of living plants. This lack of features has led in the past to the classification of a collection of unrelated fungi such as *Rhizoctonia s. lato* (Moore, 1987). Thus, the inclusion of a given taxa to the genus *Rhizoctonia* was based for a long time on the possession of certain vegetative characters such as brown pigmented hyphae, constrictions at branch points forming right angles and absence of mitospores. Together with these features, always present, there are other characters not constantly present in the entire species complex, but present in a large number of species, such as the presence of monilioid cells and sclerotia in culture, fast rates of hyphal growth or a complex dolipore septal apparatus. Approximately 120 epithets have been assigned to the *Rhizoctonia* species complex, but taxonomic reviews have narrowed this number to 37 (Andersen and Stalpers, 1994) or 49 (Roberts, 1999), depending upon the authors.

*Rhizoctonia solani* (teleomorph = *Thanatephorus cucumeris* Frank (Donk)) is widely the most studied species within the form genus. The fungus is usually recovered from soils all over the world and is considered as a very destructive plant pathogen, with a broad host range, and causes diseases in a great variety of crops, including agronomical, ornamental and forestry species (Anderson, 1982; Sneh *et al.,* 1991). In Spain, *R. solani* reduces the production and quality of crops such as potato (Sardiña, 1945; El Bakali *et al.,* 2000, 2002, 2003), sugar beet (De Andrés *et al.,* 1998), cereals (Marín *et al.,* 1992), lettuce, cotton (Melero-Vara and Jiménez-Díaz, 1990), melon and bean (Tello *et al.,* 1985; Sinobas *et al.,* 1994). This fungus causes «damping off» in seedlings, black lesions in root and seed, stem rot and rot of plant parts in contact with soil (as in the case of melon fruits or lettuce leaves). *R. solani* can also cause foliar lesions due to the germination of basidiospores on the leaf surface (Kucharek, 2000). Other *«Rhizoctonia*-like» fungi have also been reported to cause diseases in plant crops in Spain, such as *R. croccorum* (Pers.: Fr.) D.C. (teleomorph = *Helicobasidium purpureum* Pat.) which is the causal agent of violet root rot of carrot, sugar beet and saffron (Dominguez García-Tejero, 1951; De Andrés, 1998).

Classification of the different *Rhizoctonia* taxa has evolved mainly from studying the isolates obtained from diseased plants. However, the criteria and methodology employed for characterization of the strains have evolved through the years. In this sense, before the 70s, most of the agronomically important isolates of *Rhizoctonia* were classified as *R. solani* based on culture features, suggesting that *R. solani* is comprised of a number of taxonomic species representing various teleomorphic states (Parmeter *et al.,* 1967). Despite the fact that new methods and techniques have been developed in fungal systematics, classification of *Rhizoctonia* species is still considered to be in a developmental stage. In general terms, systematic approaches for this group of fungi have been widely based on both the study and characterization of anastomosis groups, and determination of the nuclear condition. When teleomorphic stages were available, comparative studies of the morphology of the basidia and basidiospores have been routinely employed and, with the development and spread of molecular biology tools in systematic studies, some of these techniques have also been applied to solve taxonomical questions in the group. As a consequence, a teleomorph has not been determined for some anamorphs, while for other asexual stages a specific epithet has not been designated, especially pertinent in the genus *Ceratobasidium.*

## Systematics of *Rhizoctonia* species

***Taxonomical survey of the form genus.*** As induction of teleomorphic stages under laboratory conditions has been difficult for this group of fungi, their characterization is primarily based on the comparison of a limited number of anamorphic features and cytological probes, such as nuclear staining, which has often resulted in much confusion. Thus, current systematic concepts for the complex (Moore, 1987; Andersen and Stalpers, 1994; Roberts, 1999), segregate filamentous fungi with *Rhizoctonia*-like anamorphs into at least seven or eight anamorphic genera depending upon the authors (Table 1): *Ascorhizoctonia* Yang & Korf, *Ceratorhiza* R.T. Moore, *Chrysorhiza* Andersen & Stalpers, *Epulorhiza* R.T. Moore emend R.T. Moore & Andersen, *Opadorhiza* Andersen & R.T. Moore, *Moliniopsis* Ruhland, *Rhizoctonia* D.C. and *Thanatophytum* Nees. Connections and correspondence between these anamorphic genera and

**Table 1.** Taxonomic synopsis of the form genus *Rhizoctonia.* Segregate anamorphic and teleomorphic genera currently accepted

| Anamorph | Type species | Basionym | Teleomorph | Type species | Basionym |
|---|---|---|---|---|---|
| *Ascorhizoctonia* Yang & Korf | *A. praecox* Yang & Korf | *A. praecox* Yang & Korf, Mycotaxon 23 (1985) | *Tricharina* Eckblad | *T. gilva* (Boud. in Cooke) Eckblad | *T. gilva* (Boud. In Cooke) Eckblad, Nytt. Mag. Bot. 15 (1968): 60 |
| *Ceratorhiza* R.T. Moore | *C. goodyerae-repentis* (Constantin) R.T. Moore | *Rhizoctonia goodyerae-repentis* Constantin, Rev. Gèn. Bot. 32 (1920): 533 | *Ceratobasidium* D.P. Rogers | *C. calosporum* D.P. Rogers | *C. calosporum* D.P. Rogers, Univ. Iowa Stud. Nat. Hist. 17 (1935): 4 |
| *Chrysorhiza* Andersen & Stalpers | *C. zeae* (Voorhees) Andersen & Stalpers | *R. zeae* Voorhees, Phytopathology 24 (1934): 1929 | *Waitea* Warcup & Talbot | *W. circinata* Warcup & Talbot (Sin = *Chrysorhiza zeae* Stalpers & Andersen) | *W. circinata* Warcup & Talbot, Trans. Br. mycol. Soc. 45 (1962): 503 |
| *Epulorhiza* R.T. Moore emend Andersen & R.T. Moore | *E. repens* (Bernard) R.T. Moore emend R.T. Moore (Sin = *Tulasnella calospora* (Boud) Juel) | *R. repens* Bernard, Ann. Sci. nat. IX, ser.9 (1909): 31 | *Tulasnella* Schröeter | *T. violea* (Quél.) Bourd. & Galzin | *T. violea* (Quél.) Bourd. & Galzin, Bull. Soc. Myc. fr. 25(1909): 15 |
| *Opadorhiza* Andersen & R.T. Moore | *O. globularis* (Saksena & Vartaja) Andersen & R.T. Moore (Sin = *Sebacina sp*.) | *R. globularis* Saksena & Vartaja, Can. J. Bot. 38 (1960): 939 | *Sebacina* Tul. | *S. vermifera* Oberwinkler | *S. vermifera* Oberwinkler, Nova Hedwigia 7 (1964): 489 |
| *Moliniopsis* Ruhland. (Sin. = *Rhizoctonia* D.C.) | *M. aderholdii* Ruhland. (Sin = *Moliniopsis solani* (Kühn) R.T. Moore | *R. solani* J.G. Kühn, Die Krankheiten der Kulturgewächse: 224 (1858) | *Thanatephorus* Donk. (Sin = *Botryobasidium* Donk *p.p.)* | *T. cucumeris* (Frank) Donk | *Hypochnus cucumeris* Frank, Ver. Deutsch Bot. Ges. 1 (1833): 62 (Sin = *H. solani* Prill. & Delacr.) |
| *Tanatophytum* Nees. | *T. croccorum (Pers.: Fr.)* R.T. Moore | *Sclerotium croccorum* Pers., Syn. Meth. Fung, (1801): 119 (Syn = *R. croccorum* (Pers.: Fr.) D.C. | *Helicobasidium* Pat. | *H. purpureum* Pat. | *H. purpureum* Pat., Bull. Soc. Bot. France 32: 172 (1885) |

their respective teleomorphs, as well as the main synonyms for these names are also indicated in Table 1.

*Ascorhizoctonia* is adopted to accommodate species with ascomycetous septal apparatus and a teleomorphic phase (ascomata) similar to those produced by members of the Pezizales order (genus *Tricharina* Eckblad). The genus *Ceratorhiza* arranges binucleate *Rhizoctonia* species with teleomorphic phases belonging to genus *Ceratobasidium. Chrysorhiza* is proposed to designate the multinucleate, *Rhizoctonia*-like anamorph of *Waitea circinata* Warcup & Talbot (=*Chrysorhiza zeae* (Voorhes) Andersen & Stalpers) which has been included for a long time within the concept of *Rhizoctonia s. str.* (=*Moliniopsis)*, presuming the existence of a close relationship with imperfect stages of *Thanatephorus.* However, some authors (Stalpers and Andersen, 1996) consider this taxon to be close to *Ceratobasidium,* on the basis of the morphology of basidia and sclerotia. Another possible member of the genus could be represented by the anamorph of *Waitea nuda* Clémençon, probably co-specific with *Rhizoctonia oryzae* Ryker & Gooch. The genus *Epulorhiza* designates *Rhizoctonia* anamorphs *(R. repens* Bernard), predominantly binucleate with teleomorphic stages belonging to genus *Tulasnella* Schröeter. Andersen and Moore (Moore, 1996) proposed the name *Opadorhiza* to designate *Rhizoctonia globularis* Saksena & Vaartaja, a taxon possessing a *Rhizoctonia*-like anamorph very close to *Epulorhiza* (excepting for the morphology of septal apparatus) and a teleomorphic phase belonging to the genus *Sebacina* Tul. *Moliniopsis* Ruhland is a genus first proposed by Moore (1987) to group anamorphs of *Rhizoctonia* with perfect stages in *Thanatephorus* and *Waitea.* Subsequently, Moore (1996) restricts the concept of *Moliniopsis* to species with *Thanatephorus* teleomorph. Nevertheless, the name *Rhizoctonia* is actually conserved against *Moliniopsis,* to name *R. solani,* the most known and studied taxa in the complex. Some authors (Moore, 1996; Stalpers and Andersen, 1996; Stalpers *et al.,* 1998) proposed *R. solani* as the type species of genus *Rhizoctonia.* In addition, the original type species of the genus, *R. croccorum* (teleomorph *Helicobasidium)*, is actually considered to be a member of the order Platygloeales. Thus, adoption of the epithet *Thanatophytum* (a previous synonym of *Rhizoctonia)* is required to designate the correct name of the anamorph taxa in *Helicobasidium.*

***Genus Thanatephorus*** *(Rhizoctonia s. str.)*. The genus *Thanatephorus* (*Ceratobasidiaceae,* Ceratobasidiales, Basidiomycota), was initially proposed by Donk (1956) to designate teleomorphic phases of the *Rhizoctonia solani* multinucleate anamorph. It is commonly accepted that *Thanatephorus* applies to most parasitic fungi (as in the case of *R. solani)* with hypochnoid, sometimes gelatinized basidiomata possessing a hymenium made up of successive layers of basidia rising from vertically branching, cymose hyphae just above basal hyphae, sometimes swollen but commonly less than twice the width of adjacent hyphae at sub-basal septum (Roberts, 1999). Somatic hyphae in *Thanatephorus* are constantly wider (more than 10 μm in diameter) (Roberts, 1999) than in *Ceratobasidium,* a closely related genus in the family *Ceratobasidiaceae* described below.

The morphology of *Botryobasidium* Donk (Donk, 1956) differs from *Thanatephorus* owing to the presence of short-sterigmate basidia, no repetitive basidiospores and the absence in culture of monilioid cells or sclerotia. Furthermore, Langer (1994) has provided evidence in *Botryobasidium* of septal pores with continuous parenthesomas, in contrast with discontinuous parenthesomas in both *Thanatephorus* and *Ceratobasidium.* Donk (1956) simultaneously established the genera *Thanatephorus* and *Uthatobasidium,* reserving the later epithet for taxa similar to *Thanatephorus,* but saprophytic and not producing sclerotia. Furthermore, Talbot and Keane (1971) proposed the name *Oncobasidium* P.H.B. Talbot & Keane for plant pathogenic taxa similar to *Thanatephorus* but not producing sclerotia. Finally, authors like Roberts (1999), considered these two genera to be synonyms of *Thanatephorus,* assuming that parasitism in this genus is considered to be facultative *(T. cucumeris* isolates are commonly reported to occur as saprotrophs), and generic distinction could be considered as weak for these three names. Other genera close to *Thanatephorus* have been recently synonymized by Roberts (1999), including *Ypsilonidium* Donk, *Cejpomyces* Svrcek & Pouzr., *Aquathanatephorus* C.C. Tu & Kimbr. (=*R. solani* AG1) and *Tofispora* G. Langer.

Evolutive relationships between *Thanatephorus* and its close relative *Ceratobasidium* remain controversial. Employing classical taxonomic approaches, some authors (Stalpers and Andersen, 1996; Roberts, 1999) have considered both genera to be part of a generic

complex, where delimitation among them presents some difficulties, and differences in morphometrical features and ecological behaviour are gradual along the several taxa within both genera. Roberts (1999) considered, after studying the type material for all accepted taxa of both genera, in combination with a preliminary ITS-based molecular phylogeny of selected species, that the two genera should be considered as synonyms. Recently, González *et al.* (unpublished), in an ITS-based phylogeny of family *Ceratobasidiaceae* (including taxa from *Ceratobasidium,* most accepted *R. solani* anastomosis groups and sequences from genus *Waitea)*, suggested that both genera, although closely related, must be retained as independent entities within *Ceratobasidiaceae.* The phylogenetic reconstruction carried out also demonstrated the convenience of segregation, in accordance with some authors (Boidin *et al.,* 1998; González *et al.,* 2001), of *Rhizoctonia solani (Thanatephorus cucumeris)* into at least four different biological species. Thus, molecular analyses suggested that *Thanatephorus praticola* Kotila & Flentje could be assigned to define, at a specific level, AG 4 isolates (and their subgroups); *T. sasakii* (Shirai) C.C. Tu & Kimbr. could represent the valid epithet to name isolates from AG 1-IA and AG 1-IC; *T. microsclerotium* (G.F. Weber) Boidin could represent AG1-IB strains, while the rest of AGs actually defined, should be confined to *Thanatephorus cucumeris s. str.*

***Genus Ceratobasidium (binucleate Rhizoctonia).*** The genus *Ceratobasidium (Ceratobasidiaceae,* Ceratobasidiales, Basidiomycota) was initially proposed by Rogers (1935) to accommodate four taxa *(C. calosporum* Rogers, the type species of the genus designated by him, *C. cornigerum* (Bourd.) Rogers, *C. sterigmaticum* (Bourd.) Rogers and *C. obscurum* Rogers), some of them usually included as part of a complex mixture of genera and species arranged in the several groups and sections recognized for wide ancient genera like *Corticium* or *Hypochnum.* Thus, two of the above mentioned taxa, *C. cornigerum* and *C. sterigmaticum* formed part of section *Botryoidea* of *Corticium.* As mentioned elsewhere above, Donk (1931) was the first author to segregate part of the Ceratobasidiales, erecting the genus *Botryobasidium* Donk within the family *Tulasnellaceae,* due to the presence in members of the new genus of basidiospores capable of germinating by repetition, a diagnostic feature in phragmobasidiate fungi. Later, Rogers (1935) suggested such a taxonomical concept by adding *Ceratobasidium* to this group of fungi. Martin (1948) equally defined the family *Ceratobasidiaceae* to accommodate the genus. Donk (1956), being conscious that *Botryobasidium* still contained certain heterogeneity of "holo-" and "heterobasidiate" taxa, segregated these last elements (species with autoreplicative spores and large sterigmata) into two genera, *Thanatephorus* and *Uthatobasidium* Donk, which were subsequently included by Jülich (1981) within his concept of Ceratobasidiales. Both *C. sterigmaticus* and *C. obscurum* are considered to belong to *Thanatephorus* in the modern concept of the genus, and are excluded from *Ceratobasidium* (Roberts, 1999). Donk (1958) erected the genus *Koleroga* to accommodate *K. noxia* Donk, a species morphologically close to *Ceratobasidium,* except for the absence of autoreplicative spores. Talbot (1965) demonstrated the presence of this type of spore in some collections of *K. noxia.* Subsequently, some authors (Roberts, 1999) considered the genus *Koleroga* as a nomenclatural synonym of *Ceratobasidium (C. noxium)*. Currently, there are between 10 (Roberts, 1999) and 11 (Kirk *et al.,* 2001) species accepted for the genus.

Species of *Ceratobasidium* are characterized for the presence of a non-sporulating, *Rhizoctonia*-like (genus *Ceratorhiza)* anamorphic phase, binucleate somatic hyphae (uninucleate in *Ceratobasidium bicorne)* and saprophytic, mycorrhizal or parasitic teleomorphic phases. *Ceratobasidium* taxa produce effuse fruitbodies of ceraceous consistency, with globose to sphaeropedunculate basidia, produced directly from basal hyphae or in raceme-like groups, usually showing a division between hypo- and epibasidium, producing basidiospores with high rates of repetitive germination (Rogers, 1935).

This set of diagnostic characters (mostly referred to hyphal cytology and nutritional behaviour), differentiate *Ceratobasidium* from *Thanatephorus.* Concerning the nomenclature of anamorphic stages of the genus, only the above mentioned genus *Ceratorhiza* is considered to date, to be the correct name to designate anamorphs with *Ceratobasidium* teleomorph (Roberts, 1999).

From an ecological point of view, the genus includes saprophytic, symbiotic and even parasitic taxa. Thus, most species have been described as saprophytic on soil or plant debris (wood and leaf litter from both

angiosperm and gymnosperm hosts), or as forming part of the fungal component of orchid mycorrhizae. A small number of taxa have been reported as parasites of herbaceous plants (some of them of economic interest) or bryophytes.

Regarding its evolutive relationships, the genus could represent for some authors (i.e. Rogers, 1935) a transitional evolutive line to modern basidiomycetes, from typically heterobasidiate (with clearly segmented basidia, possessing hipo- and epibasidia), resembling *Tulasnella*-like forms (probably the closest heterobasidious relative to *Ceratobasidium)*, towards typically holobasidiate forms with non-segmented basidia and true sterigmata. In this sense and in accordance with its current systematic position (Roberts, 1999; Kirk *et al.,* 2001), the family *Ceratobasidiaceae* could represent the most primitive group of holobasidiomycetes, with hymenial structures showing morphologies where segmentation of the basidia is still easily observed, and partition on sterigmata occurs. Studies on the ultrastructure of septal apparatus in *Ceratobasidium* and *Thanatephorus,* have revealed their affinities with the remaining holobasidiate basidiomycetes. In this sense, Binder *et al.* (2005) have recently reported phylogenetic evidence of the relationships of the Ceratobasidiales with the remaining holobasidiomycetes.

***Other Rhizoctonia-like groups.*** Among the teleomorphs connected in the literature with *Rhizoctonia*-like anamorphs, *Thanatephorus* and *Ceratobasidium* are by far the most studied, since members of both genera are pathogenic to numerous crops worldwide. However, there are other taxa with *Rhizoctonia*-like anamorphs, usually studied under the ancient concept of *Rhizoctonia s. lato.* Thus, several *Rhizoctonia*-like strains can be referred to the teleomorphic genus *Waitea* Warcup & P.H.B. Talbot *(W. circinata* Warcup & P.H.B. Talbot), which has a multinucleate anamorph, *Chrysorhiza zeae* (Voorhees) Andersen & Stalpers (=*Rhizoctonia zeae* Voorhees). This taxon is considered a lesser pathogen, causing «sclerotial rot» in sweet corn, «sheath spot» in rice or «bare patch» diseases on turfgrass (Sneh *et al.,* 1991). Recently, *Waitea circinata* has been regarded as a species complex, and split into three varieties (Leiner and Carling, 1994); var. *circinata,* var. *zeae* and var. *oryzae,* on the basis of existing differences in colony morphology of the vegetative state. In addition, Toda *et al.* (2005) reported a new disease on bentgrass caused by *W. circinata* var. *circinata,* and also found molecular support for considering three varieties within *W. circinata.*

Another two pathogenic taxa with *Rhizoctonia*-like anamorphs are members of the order Platygloeales (Urediniomycetes). Thus, *Helicobasidium purpureum* Pat. and *Helicobasidium longisporum* Wakef. are considered as the causal agents of «violet root rot» in carrots, sugar beet or saffron (Valder, 1958; Segawa and Harada, 1990).

Species of the *Rhizoctonia* complex are usually reported to be the fungal component of orchid mycorrhiza in many taxa of these flowering plants. This mycorrhizal association in terrestrial orchids is considered as endomycorrhizal (rather than ectomycorrhizal), due to the fact that hyphae from these fungi are found within cells in orchid protocorms and roots, not surrounding these plant tissues intracellularly. *Rhizoctonia*-like genera known to establish symbiotic relationships with members of the *Orchidaceae* are *Ceratobasidium, Thanatephorus* (Ceratobasidiales), *Sebacina* (Exidiales) and *Tulasnella* (Tulasnellales) (Andersen and Rasmussen, 1996).

## Biology of *Rhizoctonia* species

***Anastomosis groups in the Rhizoctonia species complex.*** A system of anastomosis grouping based on hyphal fusion has been widely accepted over the last 35 years, as the basis for recognizing groups and taxa among the several fungi that constitute the form genus (Ogoshi, 1975; Anderson, 1982; Sneh *et al.,* 1991). These methods have been applied to the different taxonomic entities of *Rhizoctonia,* including isolates of *R. solani,* binucleate *Rhizoctonia* species (Oghosi *et al.,* 1983a) or *Rhizoctonia* isolates with teleomorph belonging to genus *Waitea.*

A hyphal anastomosis reaction (Fig. 1) represents an expression of somatic or vegetative incompatibility (Anderson, 1982) and, from a biological point of view, is part of the several mechanisms involved in compatibility and sexual recognition processes, that allow the preservation of unique heterokaryons in fungi. As in most of the filamentous fungi studied, it was demonstrated in *T. cucumeris* AG 1 that mating processes (formation of heterokaryotic tufts between paired homokaryons) occurred independently of

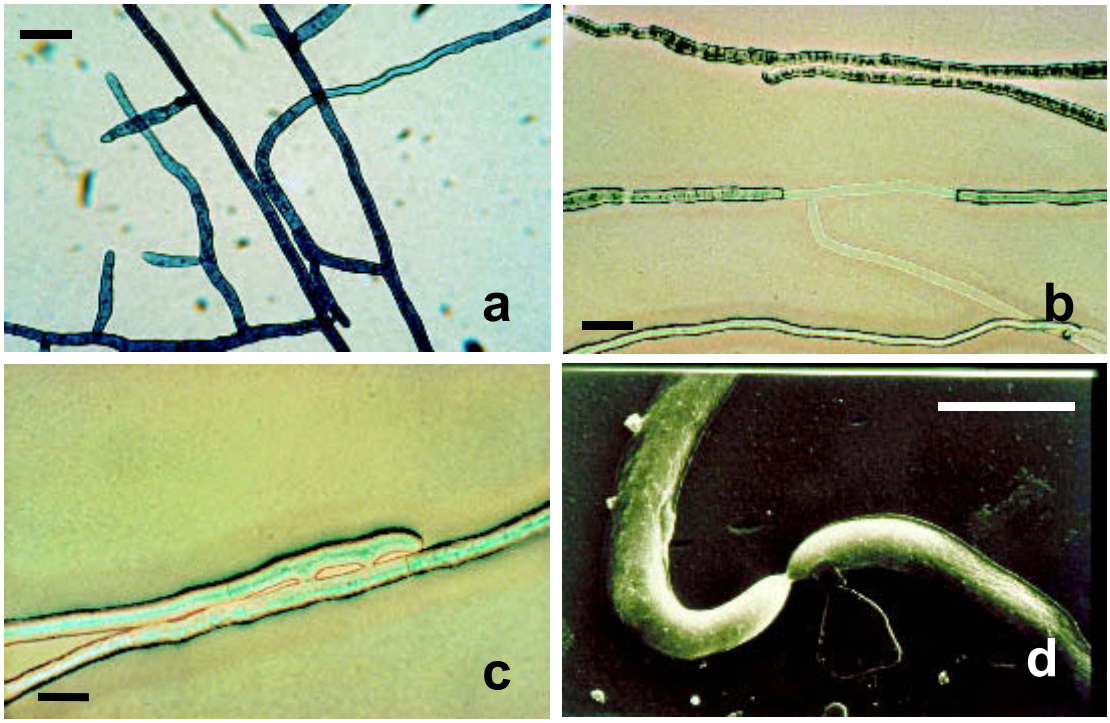


**Figure 1.** Anastomosis reactions in multinucleate *Rhizoctonia solani* strains. a, No fusion. b, fusion with death of fused cells. c and d, perfect fusion. Bars = 10 μm.

vegetative incompatibility processes (lysis of anastomosed cells). Thus, in *T. cucumeris* AG 1 sexual and vegetative incompatibility are two mechanisms that operate independently (Julián *et al.,* 1996). An anastomosis group is represented by a collection of genetically-related isolates, according to their capability to anastomose hyphae among them. These reactions can vary from a complete fusion between hyphae, including cell walls and cytoplasmic membranes (the common situation found in anastomosis reactions in one given isolate with itself), to a complete absence of reaction. Reactions in which cell walls, and probably cytoplasmic membranes, connect but no fusion occurs (generally followed by death in the connected and adjacent cells), are typical among members of the same anastomosis group.

Currently, there are several accepted classifications based on the anastomosis group (AG) concept for both multinucleate *(Thanatephorus)* and binucleate *(Ceratobasidium)* taxa within the *Rhizoctonia* species complex (Carling, 1996). In the first group of taxa, 14 anastomosis groups have been described (Table 2) (Carling *et al.,* 1999, 2002a), including 13 different groups (named from AG 1 to AG 13) whose members are generally only capable of fusing hyphae among themselves. There is another anastomosis group named AG BI («bridging isolate») that includes isolates capable of fusing hyphae among themselves and also with members of other AG. Currently, AG BI is thought to be a member of AG 2, that could suggest a paraphyletic origin for this AG. According to recent studies (Carling, 2000; Carling *et al.,* 2002b), AG BI may not represent the only «bridging isolate» group, as new isolates have been described with the same behaviour in some of the classical AGs (i.e. AG 3, AG 6, etc.). Moreover, some of these AGs described for *R. solani* isolates have been further subdivided in anastomosis subgroups (i.e. AG 1, AG 2, AG 4, AG 6 and AG 9) (Table 2), based on criteria different to anastomosis pairing, including pathogenicity, colony morphology, DNA complementarity, pectic zymograms, etc. (Carling, 1996).

As for the multinucleate taxa in the complex, anastomosis reactions have also been the main criteria to delimit and group binucleate *Rhizoctonia* taxa. Thus, those isolates of *Rhizoctonia s. lato* with *Ceratorhiza*

**Table 2.** Summary of the different groups and subgroups recognized for multinucleate *Rhizoctonia solani* isolates. Names between question marks are suggested to be biological species different to *Thanatephorus cucumeris*

| Group/Subgroup | Diseases | Teleomorph |
|---|---|---|
| AG 1 IA | Rice, corn, sorghum, bean, soybean, turfgrass, camphor seedlings | *Thanatephorus cucumeris* (=*Corticium sasakii; Hypochnum sasakii; Pellicularia sasakii)*<br>*T. sasakii*? |
| AG 1 IB | Bean, rice, soybean, leguminous woody plants, lettuce, hortensia, cabbage | *T. cucumeris*<br>*T. microsclerotius*? |
| AG 1 IC | Buckwheat, carrot, soybean, flax, pine | *T. cucumeris* |
| AG 2-1 | Crucifers, strawberry, tulip | *T. cucumeris* |
| AG 2-2IIIB | Rice, mat rush, ginger, turfgrass, corn, sugarbeet, *Chrysanthemum* | *T. cucumeris* |
| AG 2-2IV | Sugarbeet, turfgrass | *T. cucumeris* |
| AG 3 | Potatoes, tobacco, tomato, egg plant | *T. cucumeris* |
| AG 4 (HGI, HGII and HGIII) | Tomato, pea, potato, soybean, onion, cotton, snap bean, Loblolly pine seedlings | *T. cucumeris* (=*Pellicularia praticola)*<br>*T. praticola*? |
| AG 5 | Potato, turfgrass, bean, soybeans | *T. cucumeris* |
| AG 6 (HG-I and GV) | Non pathogenic | *T. cucumeris* |
| AG 7 | Soybeans | *T. cucumeris* |
| AG 8 | Poaceae | *T. cucumeris* |
| AG 9 (TP and TX) | Crucifers, potatoes | *T. cucumeris* |
| AG 10 | Non pathogenic | *T. cucumeris* |
| AG 11 | Wheat | *T. cucumeris* |
| AG 12 | Cauliflower, radish | *T. cucumeris* |
| AG13 | Non pathogenic | *T. cucumeris* |
| AGBI | Non pathogenic | *T. cucumeris* |

anamorph and teleomorph (when known) belonging to the genus *Ceratobasidium* described mainly by Japanese authors, have been assigned to 17 anastomosis groups, named from AG A to AG Q (Ogoshi *et al.,* 1983a), while the different binucleate strains defined and characterized in the USA were grouped into seven anastomosis groups, named from CAG-1 to CAG-7 (Burpee *et al.,* 1980a,b). Ogoshi *et al.* (1983b) observed by means of anastomosis testsamong both groups of isolates, that the American isolates fit well with most of the 17 Japanese groups, with the exception of CAG-5 and CAG-7, which were then named AG R and AG S, respectively. Recently, Priyatmojo *et al.* (2005) described two new groups of binucleate *Rhizoctonia* isolates causing root and stem rot of cut-flower roses, and characterized them as two new binucleate anastomosis groups, AG T and AG U, respectively. Furthermore, AG U has also been found on azalea in Missisippi by Copes *et al.* (2005).

From a biological perspective, the different anastomosis groups described in binucleate *Rhizoctonia* represent a highly heterogeneous group of fungi, due to the fact that taxonomic relationships between these isolates are difficult to associate or assign to a specific teleomorph. Table 3 shows all the binucleate *Rhizoctonia* anastomosis groups described to date,

**Table 3.** Summary of the different anastomosis groups recognized for binucleate *Rhizoctonia* isolates up to date (Sneh *et al.,* 1991; Priyatmojo *et al.,* 2005)

| Anastomosis group | Anamorph | Teleomorph |
|---|---|---|
| AG A[1] (American CAG2)[2] | *R. candida; R. endophytica var. endophytica; R. fragariae; R. ramicola* | *Ceratobasidium cornigerum;* (=*C. ramicola*) |
| AG Ba[1] | *R. fumigata* | *C. setariae* |
| AG Bb[1] | *R. oryzae-sativae* | *C. oryzae-sativae* |
| AG B(o)[1] | Unknown | *C. cornigerum* |
| AG C[1] | *R. globularis* | *C. cornigerum* |
| AG D[1] (American CAG1)[2] | *R. cerealis* | *C. cereale* |
| AG E[1] (American CAG3, CAG6)[2] | *R. muneratii* | *Ceratobasidium* sp. |
| AG F[1] (American CAG4)[2] | Unknown | *Ceratobasidium* sp. |
| AG G[1] | *R. fragariae* | *Ceratobasidium* sp. |
| AG H[1] | Unknown | *Ceratobasidium* sp. |
| AG I[1] | *R. fragariae* | Unknown |
| AG J[1] | Unknown | *Ceratobasidium* sp. |
| AG K[1] | Unknown | *Ceratobasidium* sp. |
| AG L[1] | Unknown | *Ceratobasidium* sp. |
| AG M[1] | Unknown | *Ceratobasidium* sp. |
| AG N[1] | Unknown | Unknown |
| AG O[1] | Unknown | *Ceratobasidium* sp. |
| AG P[1] | Unknown | *C. cornigerum* |
| AG Q[1] | Unknown | *C. cornigerum* |
| AG R[1] (American CAG5)[2] | Unknown | *Ceratobasidium* sp. |
| AG S[1] (American CAG7)[2] | Unknown | *Ceratobasidium* sp. |
| AG T[3] | Unknown | Unknown |
| AG U[3] | Unknown | Unknown |

[1] AGs recognized in Ogoshi *et al.* (1983a,b). [2] AGs recognized in Burpee *et al.* (1980a,b). [3] AGs recognized by Priyatmojo *et al.* (2005).

according to the nomenclature employed in Sneh *et al.* (1991). Equivalences between Japanese and American groups, anamorphs and teleomorphs (when known) are also included in this table for each AG.

The taxonomical status of the different anastomosis groups described for *Rhizoctonia* is controversial. A correlation between the concept of AG and biological species has been proposed, although these biological species are insufficiently known in *Rhizoctonia,* due to the lack of morphological characters exhibited by members of the complex, or the absence of data on the systems involved in sexual compatibility mechanisms of these fungi (Carling and Sumner, 1992).

Adopting an approach based on population genetics, some studies (Adams, 1988, 1996; Vilgalys and Cubeta, 1994) have proposed the hypothesis that the different AGs could represent genetically isolated populations within each collective taxon of *Rhizoctonia,* where intersterility systems (IS) could limit and/or prevent sexual exchange between reproductively isolated groups. According to this view, the different anastomosis groups and subgroups, could

probably be groups generated by means of IS. Advances in the knowledge of IS could lead to an understanding of speciation mechanisms in *Rhizoctonia,* due to the fact that the above mentioned authors have proposed IS groups of *R. solani* as emergent species or in current speciation processes.

***Characterization and reproduction of taxa within the Rhizoctonia species complex.*** The identification and characterization of different taxa within this group of fungi has been based on the comparison of mycelial structures observed on nutrient media *in vitro.* Taxa from the complex share a number of common features in their somatic hyphae, such as the possession of brown coloured, septated, wide hyphae, with lateral branching originating in right angles and constrained at branching points, existence of monilioid cells in culture, sclerotia, etc. In general terms, the systematics of higher fungi has been based on the measurement and comparison of morphological characters of sexual stages. In the case of *Rhizoctonia* species, such teleomorphic phases have been difficult to induce (Warcup, 1981). Thus, most identification routines in *Rhizoctonia*-like taxa have been based on studying vegetative hyphae. Recent studies (Andersen, 1990) have shown that, although identification procedures based on anamorph morphology are still required for preliminary characterization (Sneh *et al.,* 1991), additional characters are also required, given the inherent variation in these fungi, which is influenced by the availability and type of nutrients, age of cultures, moisture and many other environmental factors.

Concerning such classification systems of *Rhizoctonia* species based on anamorphic features, a number of studies have been based on analysing the number of nuclei per cell in somatic hyphae (Fig. 2) (Saksena, 1961; Flentje *et al.,* 1963; Parmeter *et al.,* 1967; Tu *et al.,* 1969). Recent studies on the characterization of nuclear condition for some *Rhizoctonia*-like taxa have shown that nuclear number could vary among species of the same genus or even within the same isolate. For example, Hietala *et al.* (1994) reported uninucleate *Rhizoctonia* isolates from nursery grown conifer seedlings, and characterized them as belonging to *Ceratobasidium bicorne.* These and other findings on the nuclear behaviour of *Rhizoctonia*-like taxa suggests the limitation of this cytological feature for taxonomic purposes. Moreover, some authors have investigated a possible correlation between cytochemical features of hyphae or resistance structures (sclerotia) and sexual stages (Tu and

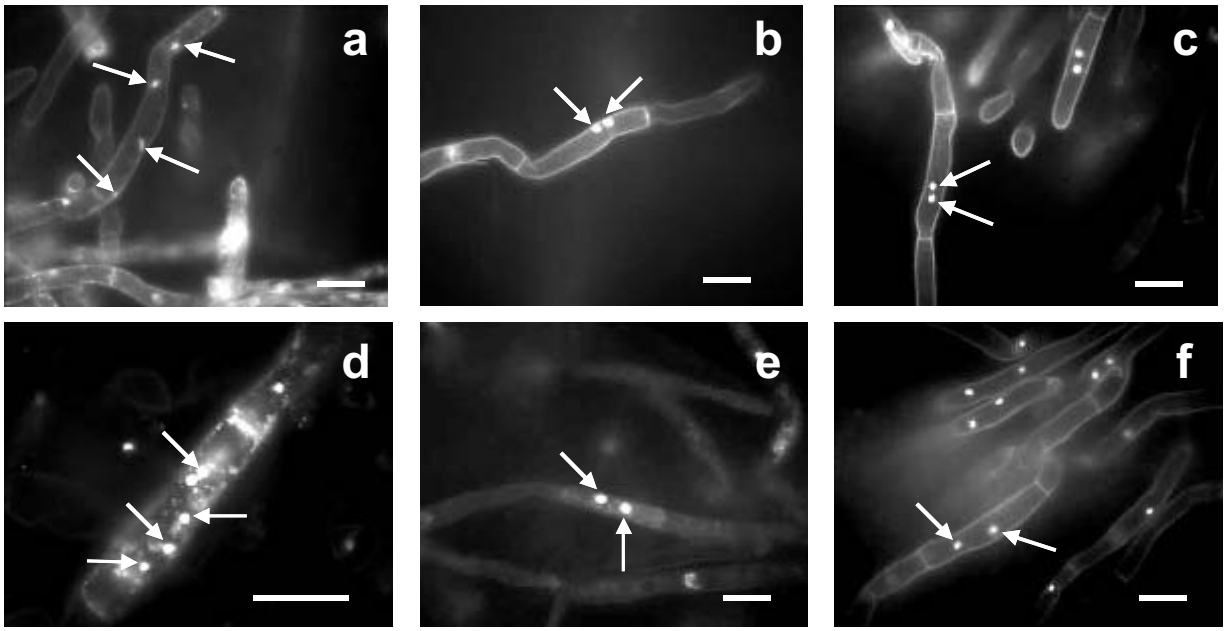


**Figure 2.** Nuclear staining of somatic hyphae in some *Rhizoctonia*-like taxa, according with the staining method described by Julian *et al.* (1997). a, *Rhizoctonia solani* AG 4. b and c, *Ceratobasidium albasitensis.* d, *Rhizoctonia solani* AG 2. e, *Rhizoctonia croccorum.* f, *Ceratobasidium cornigerum.* Bars = 10 μm.

Kimbrough, 1975). More recently, several authors (Moore, 1978, 1990) have focused on the relationship existing between the ultrastructure of certain structures such as septal apparatus of the several taxa of the complex and their systematic placement.

As indicated above, one of the main obstacles that has hampered research into the *Rhizoctonia* species complex, is the limited or null capability of the different isolates to produce sexual fruitbodies on natural substrates or in the laboratory. Most routine identification procedures in *Rhizoctonia s. lato* are carried out with sterile cultures, usually isolated from diverse environmental samples (soil, roots, plant debris, etc.). The application of methods to induce sexual fruitbodies *in vitro* (Fig. 3) has represented a valuable tool for developing the systematics of the group.

The specific environmental factors required to form sexual reproductive structures in these fungi are not well understood. Due to their phylogenetic heterogeneity, these environmental conditions differ among taxa, and even among isolates belonging to the same species. Moisture seems to be essential for the production of teleomorphs in *Rhizoctonia* spp., although the optimal relative humidity could range between 40-100% (Kotila, 1945; Sims, 1956). Concerning air exchange, Adams and Butler (1983) reported that the intake of $O_2$ and an efficient removal of $CO_2$ are required for sexual sporulation. A temperature range from 20 to 30°C has been reported as optimal for sexual fruiting in the literature (Kotila, 1947; Flentje, 1956). Moreover, variations in day/night temperatures also seem to play an important role in fruiting. Thus, the higher rates of sporulation are usually found by night, followed by a drop in diurnal temperatures. This deduction is coherent with the observation of some authors (Uchida *et al.,* 1986) that, in *Rhizoctonia* species, light stimulates hymenial formation but inhibits the ripening of basidia. Regarding the source of inoculum, age, size and form of fungal material could influence sexual fructification in isolates of *Rhizoctonia s. lato.* Finally, fruiting rates also depend on the type of nuclear condition of the isolates assayed, due to the fact that sometimes tested strains consisted in haploid somatic hyphae, unable to produce sexual propagules. In this sense, the sexuality of some *Rhizoctonia*-like fungi remains controversial. Thus, in the case of *Thanatephorus cucumeris,* mating

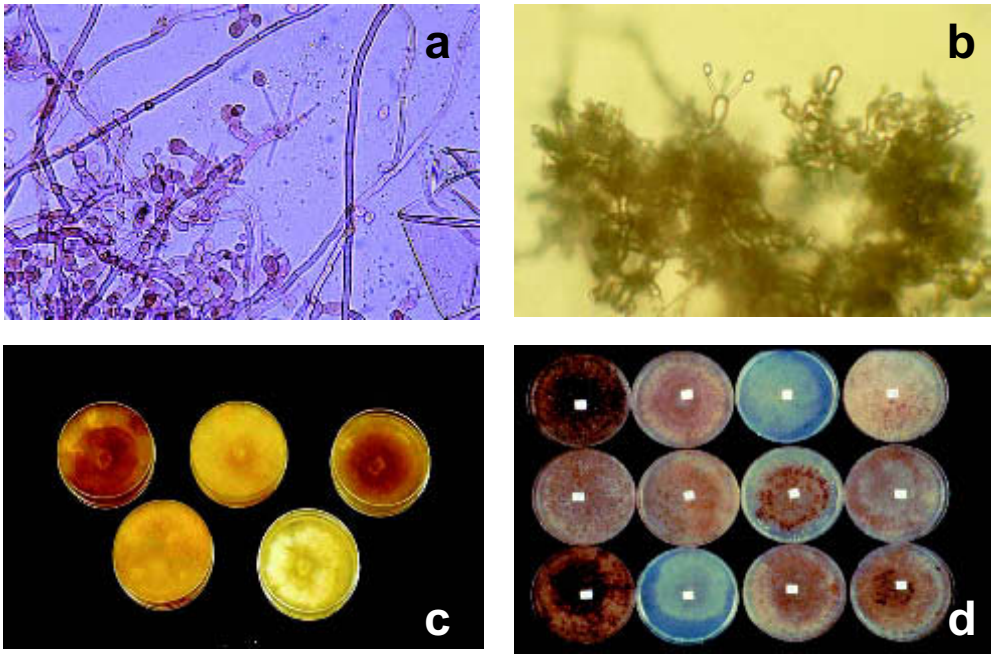


**Figure 3.** Macromorphological aspect and teleomorph formation on plate culture (water agar) of some *Rhizoctonia* isolates. a and c, *Ceratobasidium albasitensis.* b and d, *Rhizoctonia solani (Thanatephorus cucumeris)* AG 1 IC. Bars = 10 µm.

systems among the several AG have been studied, and the different groups have been found to have either homothallic (self-fertile) or heterothallic (bipolar) mating systems (Cubeta and Vilgalys, 1997). Heterothallic behaviour has been demonstrated or presumed for *R. solani* AG 1 IC, AG 4 and AG 8 (Adams, 1996), while homothallic mating has been reported for some AG 1 subgroups (Whitney and Parmeter, 1963), AG 2, AG 3 (Flentje and Stretton, 1964) and AG 4 (Adams and Butler, 1982). Regarding other groups of *Rhizoctonia*-like fungi, little is known about the sexuality of these taxa to date. In the study of Hietala *et al.* (2003), these authors described a possible homothallic behavior for *C. bicorne,* a uninucleate *Rhizoctonia*-like fungus described as causing root dieback in nursery-grown conifer seedlings.

For most researchers, nature and type of substrata could constitute the main factor for *in vitro* induction of teleomorphs. These sexual stages have been induced in cultures on soil, plants, synthetic agars and even water. In general, all the methods for inducing the teleomorph employed in *Rhizoctonia* species and other filamentous fungi, are based on providing artificially environmental stress conditions to the fungi, usually caused by a lack of nutrients or related to the existence of a strong hydrophobicity gradient in the colonizing substrates. These situations stimulate the production of sexual reproduction structures in the fungus, as a response to the new ecophysiological conditions imposed. Most of the common techniques employed for inducing sexual sporulation in *Rhizoctonia* spp. can be summarized in three main methods, depending upon the methodological basis employed:

**1. Transferring isolates from rich nutrient agar to poor nutrient agar.** This method has been widely employed, with numerous modifications of the original protocol for *Rhizoctonia,* originally described by Muller (1923). Thus Kotila (1929), Hawn and Vanterpool (1953), Flentje (1956), Murray (1982, 1984) and Adams and Butler (1983) developed variants to this method, mainly on the composition of the rich media employed. Some other recent modifications to this method (Hietala *et al.,* 1994; González *et al.,* 2002) include the transfer of isolates from rich media to plates containing sterile distilled water and plant seedlings.

**2. Soil covering methods.** According to this protocol, fruitbodies are produced in the external surface of a soil layer lying just above the agar substrates, previously colonized by the mycelia. Modifications to this method (Flentje, 1956; Stretton *et al.,* 1964; Ogoshi, 1975; Oniki *et al.,* 1985) are based on the use of different soil types, in combination with several synthetic media on which the isolates are grown.

**3. Infection in plants or plant debris.** These techniques include either the incubation of plants (or plant fragments) naturally colonized by the fungus in a moist chamber, the addition of fragments (usually leafs or twigs) or certain plants in plates with synthetic media with growing isolates, or the infection of plants in greenhouse trays containing sterile substrata previously inoculated with the fungus (Flentje, 1956).

***Molecular approaches to study the form genus Rhizoctonia.*** The development of biochemical and molecular methods for systematic purposes have significantly increased during the last few years. These methods have led to the design of more natural and evolutionary approaches to better infer phylogenetic relationships of fungi in the *Rhizoctonia* species complex. In this sense, systematics of the *Rhizoctonia* species complex has been the focus of several biochemical (Jabaji-Hare, 1996) and molecular (Cubeta *et al.,* 1996; González *et al.,* 2001, 2002) studies during the past decade.

Jabaji-Hare (1996) compiled several biochemical techniques employed with greater or lesser success in the *Rhizoctonia* species complex, including: soluble protein patterns, isoenzymes, pectic zymograms, fatty acids profiles, lectins and serological techniques (with both mono- and polyclonal antibodies). Among these, both pectic zymograms and isoenzyme profiles have been employed to identify anastomosis groups or the study of genetic relationships in members of the form genus *Rhizoctonia,* especially in *R. solani* and binucleate species. Thus, Damaj *et al.* (1993) studied the relationships between binucleate *Rhizoctonia* isolates by isoenzyme electrophoresis. Several authors (Sweetingham *et al.,* 1986; Neate *et al.,* 1988) studied the grouping and identification of binucleate *Rhizoctonia* by pectic zymograms, distinguishing at least five zymogramic groups in *Ceratobasidium cornigerum* from soil and cereal isolates. Masuhara *et al.* (1994) employed pectic zymograms in a combined study of multi- and binucleate *Rhizoctonia* isolates,

reporting that the results of this technique correlated well with previously defined AG in *R. solani,* but not for AG of binucleate isolates.

Molecular systematic studies in *Rhizoctonia* have been almost entirely confined to the molecular characterization of anastomosis groups mainly in *Ceratobasidium* and *R. solani* strains. This research has provided evidence for the genetic isolation of most of the defined anastomosis groups, suggesting, in some cases, redefinition of species concepts (Roberts, 1999). Most of these molecular techniques are based on the detection and typing of genomic polymorphisms at several levels. Some of them include DNA/DNA hybridization, G+C content analysis or PCR based methods, including those that detect polymorphisms in the genome, like RAPDs and AFLPs, or in certain genomic regions or genes, like RFLPs (for ribosomal RNA) or direct sequencing of these and other genomic regions (ribosomal DNA, actin gene, transcription elongation factor, beta tubulin gene, Ras protein, chitin synthase, etc.) (Bruns *et al.,* 1991; Mehmann *et al.,* 1994; Thon and Royse, 1999; Helgason *et al.,* 2003).

Determination of G+C content was conducted in the early 80's (Kuninaga and Yokosawa, 1980) with *R. solani* and it was established that this content was very similar (with more than 90%) in strains belonging to the same anastomosis group. A number of studies based on DNA/DNA hybridization methods (i.e. Kuninaga and Yokosawa, 1982a,b, 1983, 1984a,b, 1985a,b; Vilgalys, 1988; Carling and Kuninaga, 1990) demonstrated that grouping of several AGs in *R. solani* on the basis of sequence complementarity corresponded with anastomosis reactions. Duncan *et al.* (1993) were able to distinguish subgroups in *R. solani* AG 2 and AG 8 employing RAPD probes. Regarding binucleate *Rhizoctonia,* Toda *et al.* (1999) established that, employing both RAPDs and RFLPs, a distinction between two anastomosis subgroups from a collection of AG D isolates. Vilgalys and González (1990) found a high degree of relatedness between the restriction patterns generated by RFLPs in a collection of *R. solani* isolates, and the several anastomosis groups that they represented. Liu *et al.* (1993) suggested, based on RFLP analyses, the existence of 25 anastomosis groups in *R. solani,* in contrast with the nine existing groups reported for the taxon by this date. Regarding binucleate *Rhizoctonia* (genus *Ceratobasidium)*, Cubeta *et al.* (1991) were able to characterize 13 of the 21 anastomosis groups described for the group, employing restriction analysis of part of the rRNA 28S subunit. On the other hand, studies based on the AFLP technique, scarcely employed in *Rhizoctonia,* were based on several aspects related to factors and genes involved in sexual compatibility mechanisms of *R. solani* (Julián *et al.,* 1999) or investigating genetic diversity of some *R. solani* AG (Ceresini *et al.,* 2002). Sequencing of ribosomal DNA has been widely employed in the complex during recent years, to reconstruct phylogenetic relationships between the different organisms of the form genus (Boysen *et al.,* 1996; Kuninaga *et al.,* 1997; Roberts, 1999; Salazar *et al.,* 1999, 2000; González *et al.,* 2001, 2002; Pope and Carter, 2001; Shan *et al.,* 2002) or less frequently other regions such as beta-tubuline (González *et al.,* 2003). In the future, molecular approaches should include the sequencing of a broader range of DNA regions (e.g. beta-tubulin, elongation factor 1-alpha, calmodulin, chitin synthase, actin, etc.), to obtain and combine more data sets to infer and reconstruct phylogenetic relationships among members of the group. In addition, the adoption of suitable genetic markers will increase the knowledge about population biology of *Rhizoctonia s. lato* taxa, especially in topics such as genetic relatedness, gene flow, isolation or subdivision among populations, integrating these population biology studies with the existing knowledge on AG or biological species concepts.

## Pathology and hypovirulence in the complex

***Infection process in Rhizoctonia solani.*** The events occurring during the infection process of *R. solani,* include adhesion, penetration, colonization and host reaction. Experimental data available on this topic have revealed similarities among the several *Rhizoctonia solani* AGs or pathogenic *Ceratobasidium* species. Thus, a generalized description of the infection process can be outlined.

When *Rhizoctonia* hyphae contact the external surface of a compatible host, there is a recognition phenomenon that results in profuse hyphal branching and formation of infection structures. The initial steps of the infection process are characterized by both the adhesion of hyphae and an altered growth pattern,

resulting in directed hyphal growth and the formation of penetrating hyphal structures. Infection structures that are subsequently formed allow the fungus to penetrate intact plant tissue. Host specificity determined the formation of short swollen hyphae, apresoria or repetitive T-shaped hyphal branches. In their extremist form, complex infection structures can be seen as massive dome-shaped, infection cushions. In the next step several of the swollen tips simultaneously form infection pegs. The pegs will penetrate the cuticle and epidermal cell wall (Keijer, 1996). Most studies of infection in *Rhizoctonia solani* have been done with representatives of AG 1, AG 2, AG 3 and AG 4. In the infection course, substances are exchanged between the pathogen and the host plant. These include materials such as extracellular fungal enzymes and host exudates. In this sense, it has been shown that during the early stages of the infection process, *R. solani* AG 4 produces pectinolytic and cellulolytic enzymes. Furthermore, endopectinlyase has been reported to be associated with tissue degradation in later stages of the infection (Marcus *et al.,* 1986). Bertagnolli *et al.* (1996) have identified at least 10 different extracellular enzymes produced by *R. solani* AG 2-2IIIB, in infection processes associated with soybean seedling root rot. Finally, other extracellular enzymes such as pectinase, pectin lyase, cellulase, phosphatase or pectin methylesterase have been reported to be secreted by several AGs of *R. solani* (Sherwood, 1966; Lister *et al.,* 1975; Bateman and Basham, 1976). Evidence for the role played by pectinolytic enzymes in the infection process has come from the observations made by Weinhold and Bowman (1974), where these authors reported that an exogenous supply of glucose could significantly reduce lesion development on cotton. Also, the pathogenic process can be interfered by methyl glucose, suggesting that the effect can be attributed to interference with mucilage formation and adherence so that physical contact with the plant is inadequate to stimulate infection-cushion formation (Weinhold and Sinclair, 1996). After infection structure formation, penetration events are carried out directly through the cuticle and epidermal cell walls or more rarely (as in the case of *Rhizoctonia solani* AG 1) across the stomata, via fine penetration pegs of 1-2 μm in diameter (Weinhold and Sinclair, 1996). *R. solani* infections can produce cutinase, suggesting the existence of enzymatic involvement in cuticle penetration. However, levels of cutinase production must be low, since the plant cuticle generally remains intact after penetration, except in the areas of hyphal entry. After penetration, colonization of plant tissue is accomplished by the production of hydrolytic enzymes capable of degrading several cell walls beyond the advancing hyphae. Weinhold and Motta (1973) reported evidence for cell wall degrading enzyme activity prior to penetration in *R. solani* AG 4. Together with cell wall damage, changes in the cytoplasm of cortical cells can be detected before colonization events are produced. Thus, in addition to swelling and enzymatic degradation of cell walls, the cytological changes in infected plants include the formation of reaction zones, plasmolysis and collapsing of the entire cytoplasm. From a cytological point of view, pathogenesis in *R. solani* is characterized by severe damaging or killing of plant cells, before or immediately after penetration and colonization. Thus, as in other fungal pathogen models, penetration and colonization in *R. solani* is regarded as a primary process of hyphal growth into highly degraded or moribund plant tissue, suggesting a combination of both necrotrophic and hemi-biotrophic behaviour for this fungus on its compatible hosts. However, future studies on the colonization by *R. solani* isolates of non-compatible hosts, could help to define more accurately the type of trophic behaviour of this fungus.

***Extrachromosomal elements in Rhizoctonia.*** Linear DNA plasmids constitute a group of extrachromosomal elements named invertrons (Sakaguchi, 1990). These are found in fungi, usually in mitochondria, and also in bacteria. The genome structure of these invertrons in fungi is similar to some viral genomes, such as adenovirus or some bacteriophages, like *Bacillus subtilis* phage ϕ29 (Sakaguchi, 1990). Some of these linear plasmids share common sequences with mitochondrial genome, while others do not. This group of linear plasmids has been described in several fungal genera (i.e. *Agaricus* L., *Claviceps* Tul., *Fusarium* Wilt, *Neurospora* Shear & B.O. Dodge, etc.) (Samac and Leong, 1989). The other abundant type of fungal extrachromosomal elements corresponds to double-stranded RNAs (dsRNAs). Some of those elements are of viral origin (mycoviruses), with genes that code for RNA-dependent RNA polymerase associated with the virions (Tavantzis and Bandy, 1988).

One of the most widely studied taxa concerning extrachromosomal elements and degree of pathogenicity

in the complex is *R. solani.* Thus, several AGs of *T. cucumeris* have extrachromosomal elements of two main types, dsRNA molecules and linear plasmids. The role of these extrachromosomal elements in the pathogenicity of the fungus is currently being elucidated by several research groups (e.g. Bharathan *et al.,* 2005).

A plasmid of 2.7 kb has been isolated from *R. solani* AG 4, named pRS64 (Hashiba *et al.,* 1984). This research detected three plasmids (pRS64-1, pRS64-2 and pRS64-3) with the same molecular weight and high sequence conservation. These plasmids showed a linear structure with the presence of hairpin loops at both ends of the molecule. Although it was presumed that the existence of the plasmid conferred hypovirulence to the fungus, these results have not been reproduced (Miyashita *et al.,* 1990). Hybridization experiments demonstrated that these plasmids had sequence homology with chromosomal DNA regions (Wako *et al.,* 1991). The complete sequence of the pRS64-2 linear plasmid has been obtained by Katsura *et al.* (1997). However, the function of these linear plasmids in *R. solani* AG4 remains unknown. Plasmid structure of covalent ends with hairpin loops suggests replication mechanisms for the plasmid similar to those of the *vaccinia* virus. Linear plasmids have been found in nine AG groups described for *R. solani* (Jabaji-Hare *et al.,* 1994). Similar types to the pRS64 plasmids (concerning structure and mitochondrial localization) have been found in two extrachromosomal elements of *R. solani* AG 4 (of 2.4 kb) and AG 5 (of 3.6 kb) respectively. No homology has been found between the nucleotide sequence of the linear plasmids of *R. solani* and sequences deposited in public databases.

Extrachromosomal elements of dsRNA present in *R. solani* probably represent mycoviruses within the genome. Two types of these mycoviruses are currently described, Partiviridae and Totiviridae. For the first group, encoding regions for capsid protein and RNA-dependent RNA polymerase are distributed along the different dsRNA segments. In contrast, in Totiviridae, the genomic information for both proteins is encoded in the same segment. In both cases, dsRNA segments are located in the cytoplasm. Mycoviruses in *R. solani* exhibit several dsRNA fragments with varied genome size. The relationship between dsRNA segments and pathogenicity of the fungus seems to be quite complex. Thus, there is a broad range of dsRNA fragments, not only between different *R. solani* AGs, but even among isolates belonging to the same AG. Lately, in *R. solani* AG 3 a 6.4 kb dsRNA (M1) molecule has been described that induces virulence; this dsRNA exhibited six open reading frames (ORFs) with sequence homology encoding genes for helicases and binding motifs for ATP/GTP of bromoviruses (Tavantzis *et al.,* 1989), and with the cytochrome-c oxidase assembly factor (Jian *et al.,* 1998). Interestingly, no cross hybridization occurs between dsRNA fragments isolated from strains representing different AGs (Tavantzis *et al.,* 1989; Lakshman and Tavantzis, 1994, 1995). Recently, a dsRNA fragment of 3.6 kb has been characterized in *R. solani* AG 3 (Lakshman *et al.,* 1988), possessing an ORF with sequence homology with genes codifying for a RNA-dependent RNA polymerase and a truncated repressor of quimic acid pathway, which is considered as a precursor of the pathway of aromatic amino acids. Furthermore, aromatic amino acids are precursors of melanin, an essential component for virulence in *R. solani,* since melanin seems to be necessary to maintain physical rigidity of appresoria formed by infective hyphae (Tavantzis and Bandy, 1988; Tavantzis *et al.,* 1989). A review of extrachromosomal elements in *Rhizoctonia solani* and their relationship with pathogenicity can be seen in Rubio *et al.* (1996), Tavantzis *et al.* (2001) and Bharathan *et al.* (2005).

***Hypovirulent Rhizoctonia isolates as biological control agents.*** The concept of biological control has been historically linked to the phenomenon of suppression of fungal plant diseases in the soil. Thus, most research into biocontrol agents has focused on the suppression of pathogenic organisms in agricultural soils. The basis for the development and application of these agents is related to the existence (naturally or artificially induced by means of certain agricultural practices) of suppressive soils (Lucas and Sarniquet, 1990). The existence in some soils of natural populations of microorganisms, capable of preventing and controlling the spread of certain plant diseases caused by other microorganisms, represents the starting point to generalize the use of biological agents, or extracts from their secondary metabolism. For example, suppression of *Rhizoctonia* disease has been reported in several pathosystems, like the rot root caused by *Rhizoctonia* in wheat (Lucas *et al.,* 1993).

The existence of these soils revealed the nature of biocontrol processes very early on (Baker, 1990). According to classical biocontrol models, the

microorganisms are isolated from soil, some of which show evidence of control activity against pathogens *in vitro,* being more or less effective *in vivo.* Historically, a number of microorganisms have been proposed since the 70's as causal agents of disease suppression phenomena in many agricultural soils. Some of these classical agents include filamentous fungi such as *Gaeumannomyces* spp. (Tivoli *et al.,* 1974; Wong, 1975), *Phialophora* spp. (Deacon, 1976), *Trichoderma* spp. (Simon and Sivasithamparam, 1989), or bacteria like *Pseudomonas fluorescens* (Cook and Rovira, 1976) or *Bacillus* spp. (Capper and Campbell, 1986).

During recent years, a number of studies on the capability of binucleate *Rhizoctonia* species (mainly from genus *Ceratobasidium)* to use them as biological control agents have been reported. These biological control properties have been demonstrated against virulent isolates of multinucleate *Rhizoctonia* (mainly *R. solani)* and other fungal pathogens. Thus, biological protection events have been reported in a number of isolates (Sneh *et al.,* 1986; Cubeta and Echandi, 1991; Harris *et al.,* 1993; Sneh and Ichielevich-Auster, 1995; Ross *et al.,* 1998) against a broad range of plants, such as melon, tomato, lettuce, radish, pepper, potato, bean, rape, sugarbeet, etc. A complete compilation of the different protective isolates, anastomosis groups and plant species involved in the different biological protection studies with *Rhizoctonia* spp. can be obtained in Sneh (1996, 1998).

The capability of a broad range of hypovirulent or non-pathogenic isolates of the form genus *Rhizoctonia* to prevent and control certain fungal diseases, has been reported by numerous authors (i.e. Herr, 1995; Sneh, 1998). These protective isolates have usually been characterized as avirulent strains of multinucleate *R. solani* or mostly, binucleate *Rhizoctonia* (genus *Ceratobasidium)* isolates. A number of plant diseases caused by different AG of *R. solani* have been controlled at several scales by this type of biological agent (Castanho and Butler, 1978; Burpee and Goulty, 1984; Ichielevich-Auster *et al.,* 1985; Cardoso and Echandi, 1987; Herr, 1988; Escande and Echandi, 1991; Harris *et al.,* 1993, 1994). Also, protection against other fungal or even bacterial pathogens has been reported. Thus, Harris *et al.* (1993, 1994) demonstrated protection by certain binucleate isolates against *Pythium ultimum* var. *sporangiiferum,* while Sneh and Ichielevich-Auster (1995) reported similar effects against *Pythium aphanidermatum* and *Pseudomonas syringae* pv. *lachrymans.* In addition, Burns and Benson (2000) carried out biocontrol experiments with binucleate *Rhizoctonia* against *Pythium ultimum* and *Trichoderma virens* in vinca *(Catharantus roseus).* Furthermore, González *et al.* (2002) recently reported a new binucleate *Rhizoctonia* species belonging to the genus *Ceratobasidium* isolated from Spain *(C. albasitensis* V. González & V. Rubio), capable of protecting several plant species against *R. solani (T. cucumeris)* (Fig. 4) and other pathogenic fungal genera such as *Fusarium (F. solani)*, *Alternaria (A. alternata)* or *Penicillium (P. digitatum* and *P. expansum)*.

In addition to the protective effects mentioned above, it has been shown that some binucleate *Rhizoctonia* isolates increased plant growth, even in the absence of fungal pathogens (Fig. 5). Sneh *et al.* (1986) reported these effects on the growth of radish, carrot, lettuce, cotton and wheat seedlings and Harris *et al.* (1993, 1994) found similar phenomena in pepper and some ornamental species. Finally, Sneh *et al.* (1986) and Bandy and Tavantzis (1990) observed in potato seedlings inoculated with hypovirulent isolates of *R. solani* AG 3, that biomass rates were increased and early tuberization and flowering occurred compared to untreated controls. These effects on potato plants were also reported in Spain by González *et al.* (2000).

The non-pathogenic or hypovirulent *Ceratobasidium* species constitutes an important part of the group of non-sporulating *Rhizoctonia*-like fungi in soil, and in certain cases these taxa could represent 10-30% of the total *Rhizoctonia* spp. populations (Ichielevich-Auster *et al.,* 1985). Concerning the dynamics of these populations in the soil, there are few studies about the factors involved in the presence and distribution of these isolates in a given agroecosystem and the frequency of isolation of these strains is strongly dependent on the recovery methods employed. Thus, isolation methods from organic debris, seem to yield high recovery rates of hypovirulent *Ceratobasidium* isolates, due to the low selectivity of this methodology (Villajuan-Abgona *et al.,* 1996). The role and significance of *Ceratobasidium* spp. populations in the soil have not yet been investigated. However, its prevalence in the soil suggests that these populations could play an important role in the suppression of certain diseases. In spite of the existence of natural or artificial suppressive soils described in the literature, such as those attributed to *Trichoderma harzianum*

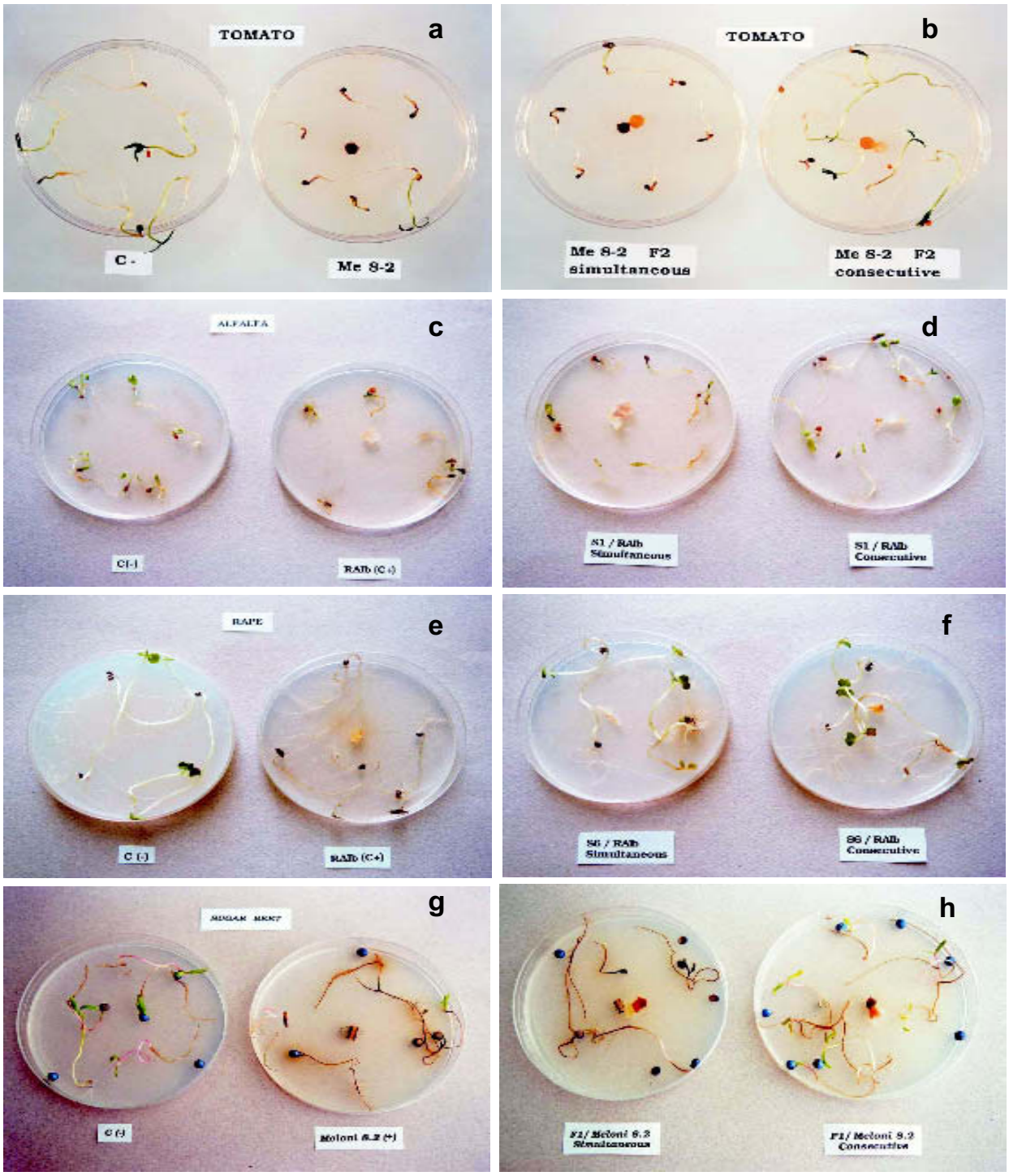


**Figure 4.** Biological protection at laboratory scale with *Ceratobasidium albasitensis* strains (F1, F2, S2 and S6) in several plant seedlings, against several *R. solani* isolates (Me-8.2 and Ralb) at two inoculation moments; both protective and pathogenic strains simultaneously, and consecutive infection of the pathogen, four days after protective isolates inoculation. a and b, tomato; c and d, alfalfa; e and f, rape; g and h, sugar beet.

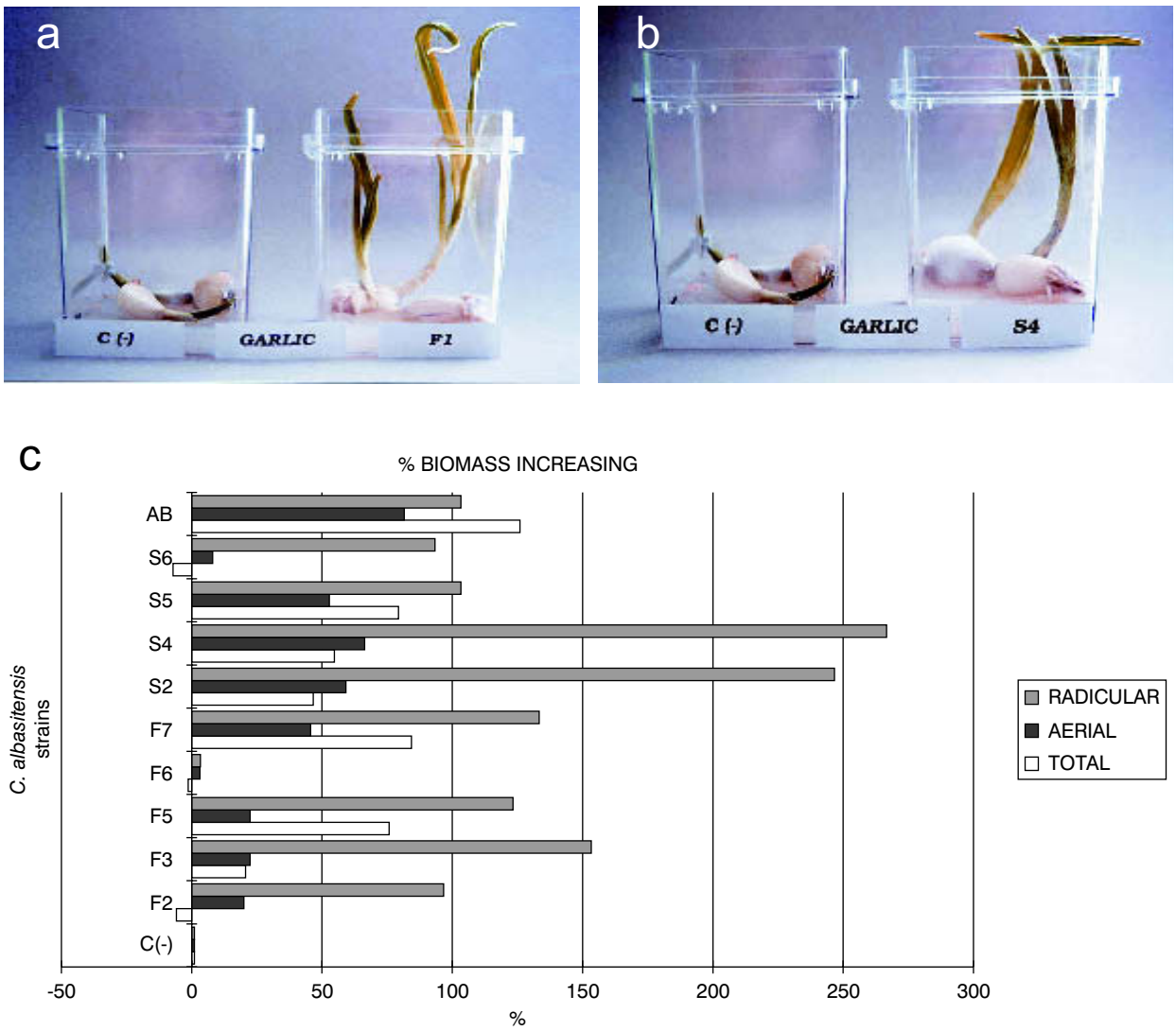


**Figure 5.** Growth promotion effects by *Ceratobasidium albasitensis* in garlic *(Allium sativum)*. a and b, laboratory scale (using *C. albasitensis* F1 and S4 strains). c, percentages of biomass increasing (radicular, aerial and the sum of both) at greenhouse scale.

Rifai (Henis *et al.,* 1978; Chet and Baker, 1981), no similar systems have been reported for members of the genus *Ceratobasidium.* However, some authors (i.e. Roberts and Sivasithamparam, 1986) reported that in wheat fields soil infested with *R. solani,* the center of disease patches was dominated by this fungus, while the populations of binucleate *Rhizoctonia* were distributed along the margins of these patches, suggesting that these isolates could be involved in controlling the spread of these disease patches by means of antagonistic phenomena against pathogenic *R. solani* strains, despite the fact that some binucleate *Rhizoctonia* isolates have been reported to be pathogens on wheat.

Regarding the genetic and physiological factors involved in hypovirulence (and virulence) in the different groups of *Rhizoctonia,* the possession of enzymes and the ability to synthesize melanin have been revealed as important. Melanin has been found to be essential in pathogenicity processes in several fungi such as *Pyricularia* or *Colletotrichum* (Bell and Wheeler, 1986), being necessary in these fungi to penetrate the host epidermis and advance across the remaining tissues. Several authors (i.e. Sneh *et al.,*

1985; Villajuan-Abgona *et al.,* 1993) have pointed out that hyphae from hypovirulent isolates from the genus *Ceratobasidium* are usually hyaline, while hyphae from pathogenic isolates of *R. solani* are usually pigmented with brown or grey tones, due to the accumulation of melanin in their cell walls. No studies have been designed, to date, to determine a possible relationship between the lack of melanin in the cell walls of some isolates of *Ceratobasidium* and its hypovirulent behaviour.

It has also been observed that the different isolates showed different protective capabilities, suggesting different protection strategies. Moreover, some authors have shown that in the protective effects of a given isolate, one or more mechanisms could be simultaneously involved. In spite of the fact that little is still known about these mechanisms (Sneh, 1996), two main groups of action have been postulated. A first group could consist of direct interactions, mainly involving horizontal transmission mechanisms of dsRNA-like mycoviruses, or direct antagonism phenomena (evidenced by competition of nutrients or infection sites, antibiosis, hyperparasitism, etc.). A second type of mechanism proposed corresponds to indirect interactions, such as the existence of physical barriers, the production of lytic enzymes or inhibitory substances such as phytoalexins or phenols, or the induction of systemic resistances (SARs) in the plant host (Poromarto *et al.,* 1998). Hence, Hwang *et al.* (2003) reported expression of systemic resistance in poinsettia against *R. solani* stem rot, induced by treating plants with binucleate *Rhizoctonia* isolates.

In summary, studies on different species, genera and families that have historically been included under the concept of the *Rhizoctonia* species complex, have been traditionally focused on the description, ecological characterization or epidemiology of plant diseases attributed to these organisms. In addition, a classification system based on hyphal anastomosis reactions has been developed during the last 70 years to classify isolates from some of the main genera of the complex. Conversely, efforts to establish a classification system for these fungi based on the comparison of morphometric characters from sexual stages have been hampered due to the low capability of these organisms to produce sexual fruitbodies in nature and in the laboratory. As a consequence, much effort has been paid to developing methods to induce formation of sexual morphs for these fungi in the laboratory, in order to provide new and reliable morphometric characters for taxonomical purposes. Together with anatomical features provided by fructifications obtained *in vitro,* the comparison of certain cytological structures (especially septal apparatus) by means of electron microscopy, has permitted more accurate and phylogenetical grouping to be developed in the form genus. The advent of molecular methods to study fungal diversity has revealed evolutionary relationships and the molecular basis of some important ecophysiological processes in several *Rhizoctonia*-like groups, such as recognition, colonization or penetration of plant tissues and facilitate the development of routine and reliable methods to identify and characterize isolates of the group from complex environmental samples. Furthermore, the discovery of some antagonistic organisms for several pathogenic *Rhizoctonia*-like fungi (including reported isolates of hypovirulent or non-pathogenic members of genera such as *Thanatephorus* or *Ceratobasidium)*, have led to a new way to control diseases caused by members of the *Rhizoctonia* species complex. The success of these biocontrol strategies, could reduce the massive employment of chemicals and favour the adoption of IPM (Integrated Pest Management) agricultural practices.

In the future, new topics and approaches will challenge research into the *Rhizoctonia* complex. These will probably include the development of new methods to understand evolutionary relationships in genetically diverse groups of the complex, the molecular bases of both infection and biological protection processes and the ecological roles played by these fungi in the ecosystems where these organisms are usually found.

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